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Clarifying the northern distributional limits of the slipper limpet *Crepidula fornicata* in the northwestern Atlantic

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Abstract: The distribution of the slipper limpet *Crepidula fornicata* (Linnaeus, 1758) in the northwestern Atlantic is generally understood to extend only as far north as Baie des Chaleurs (~48°N, 66°W) in the southwestern Gulf of St. Lawrence and only as far east as Cape Breton Island, Nova Scotia (~46°N, 60°W). Here we present evidence that this species is found considerably further north (to 51°N) and east (to 55°W) than previously recognized. More specifically, its distribution is now known to include the Quebec "Lower North Shore" of the Gulf of St. Lawrence as well as the southern and western coasts of Newfoundland. Our evidence is based upon (1) shell collections from 12 museums in Canada and the U.S., (2) reports from both the primary and the secondary literature dating back to 1841, and (3) collections of *C. fornicata* in Newfoundland in 2009. While our investigations suggest that *C. fornicata* is expanding its geographic range in eastern Canada, we cannot be certain of this since the northern Gulf of St. Lawrence, Newfoundland, and Labrador have not been extensively sampled in the past for non-commercial benthic marine molluscs. Factors such as larval drift in known surface currents may be sufficient to explain such supposed range extensions. Clarification of current geographic ranges of marine species, particularly of well-studied and easily recognizable taxa such as *C. fornicata*, remains an important task for establishing temporal benchmarks against which to assess the effect of climate change on the marine environment.

Key words: geographic range, gastropod, climate change

Climate change can impact marine ecosystems through contractions and expansions of species' geographic ranges (Southward *et al.* 1995, Jackson 2008, Cheung *et al.* 2009). Predicting the response of an organism to such environmental changes requires a good understanding of its present geographic range, its ecology, and its tolerance for temperature, salinity, oxygen levels, and turbidity (Derivera *et al.* 2007, Therriault and Herborg 2008, Cheung *et al.* 2009). Even for charismatic or well-studied marine taxa, making such predictions can be challenging given that current geographic ranges are often not well circumscribed. Assessing distributional limits can be particularly difficult for broadly dispersed taxa for which reference specimens are not well represented across their geographic range, and for which literature from past collection efforts is not widely accessible.

The slipper limpet *Crepidula fornicata* (Linnaeus, 1758) is an easily identified and widely-studied marine species with a poorly defined native geographic distribution. These snails are common in shallow subtidal (<50 m) marine habitats along the eastern seaboard of the United States, where their presence is often revealed by their characteristic "slipper-like" shells washing onshore. The geographic distribution of this species in North America is extremely broad: Malacolog, a database of western Atlantic marine molluscs (Rosenberg 2009), lists a latitudinal range of 25°N to 48°N for *C. fornicata*, with its northern range extending into three Canadian provinces, New Brunswick (NB), Prince Edward Island (PEI), and Nova Scotia (NS). Publications focusing on *Crepidula* have presented northern geographic range limits in the northwestern Atlantic associated with the southern Gulf of St. Lawrence, and more specifically PEI (Hoagland 1977, Collin 2001) or NB (Escuminac Point, NB; Blanchard 1997). These northern distributional limits are not well supported, however, and conflict, to varying degrees, with regional publications based upon faunal inventories of the Gulf of St. Lawrence (*e.g.*, Brunel *et al.* 1998). To clarify the current geographic range of this species in eastern Canada, here we document (1) distributional records published before 1934 in the widely-available English literature, (2) more recent distributional records in regionally-available literature, including those by Quebec (QC) investigators, (3) unpublished museum records from 12 museums in Canada and the U.S., and (4) the results of recent shallow-water collections of this species.

MATERIALS AND METHODS

Literature review

Our literature review began in 1989 with a species-level catalogue of all marine invertebrates recorded from the Gulf

of St. Lawrence, funded by the St. Lawrence Vision 2000 program and the Maurice Lamontagne Institute (Fisheries and Oceans Canada) in Mont-Joli, QC (Brunel *et al.* 1998). Reviews of the early literature were provided by Ganong (1887) and Whiteaves (1901) as well as earlier (from 1956) private communication with east coast scientists (*e.g.*, A. G. Huntsman, E. L. Bousfield). The systematic retrieval of new articles was subsequently achieved through accessing the *Zoological Record* back to 1902. In addition, reports and papers from the grey literature were actively searched for, especially those by authors associated with the Fisheries Research Board of Canada and its earlier designations. Papers published by the Quebec Department of Fisheries and the equivalent services in the four Atlantic provinces bordering the Gulf of St. Lawrence, including the pre-1949 Newfoundland (NL) government, were also examined. Promising titles cited in those publications were further investigated, with an emphasis on regional studies in the Gulf of St. Lawrence. Private (*e.g.*, P. Brunel, E. Bourget) and public collections (*e.g.*, Maurice Lamontagne Institute) were also used. Monographs and field guides covering the western Atlantic and the Arctic were searched for general information on geographic distributions. Only the most relevant field guides were retained in our review. The literature review for *Crepidula fornicata* and other marine invertebrate taxa of the Gulf of St. Lawrence was reported in Brunel *et al.* (1998). In 2009, we verified these older distributional records for *C. fornicata*, adding to those presented in Brunel *et al.* (1998). We also searched for recent primary research articles through Web of Science literature reviews using key words or papers citing seminal publications on *Crepidula,* such as Hoagland (1977).

Surveys of museum records, shorelines, and shallow marine habitats

We employed two additional methods to ascertain the northern range of *Crepidula fornicata* in the northwestern Atlantic. First, we examined collections from major museums and reference collections in northeastern North America, including the Academy of Natural Sciences of Philadelphia (ANSP), the American Museum of Natural History (AMNH), the Atlantic Reference Centre (ARC), the Canadian Museum of Nature (CMN), the Field Museum of Natural History (FMNH), the Maurice Lamontagne Institute (MLI), the Museum of Comparative Zoology, Harvard (MCZ), the National Museum of Natural History (USNM/NMNH), the Nova Scotia Museum of Natural History (NSMNH), the Peabody Museum of Natural History (PMNH), the Royal Ontario Museum (ROM), and The Rooms Provincial Museum (Newfoundland and Labrador; NFM). Distributional information from these 12 collections was based on inventories provided by collections' staff. For incomplete museum records from critical parts of *C. fornicata*'s range, we also obtained as much missing data as possible, especially geographic coordinates and dates of sampling. We verified databases, either personally or with the assistance of colleagues, by direct examination of specimens from some of these collections (CMN, MLI, NFM, ROM); in other cases we relied on the correct identification and record keeping of the curatorial staff. Our verification of collection information for *C. fornicata* demonstrated a high degree of reliability, likely in part because this is a well known species, but also because there are only two other species of *Crepidula* reported from eastern Canada: *C. plana* Say, 1822 and *C. convexa* Say, 1822 (Brunel *et al.* 1998, Rosenberg 2009). *Crepidula plana* is abundant, but has distinctive flat, white shells unlikely to be confused with *C. fornicata*. *Crepidula convexa,* which can be confused with small *C. fornicata,* appears to be rare within eastern Canada. Only two museum lots of this species were uncovered in our survey of the Gulf of St. Lawrence (USNM 224957; MCZ 144822); in addition, only two research publications, Verrill (1873) and Medcof and Morrison (1943), directly support its presence within this geographic region.

Second, we made new collections of *Crepidula fornicata* in 2009 and 2010. Based on literature and museum records of *C. fornicata* from NL, we explored shorelines and shallow marine habitats close to its northern distributional limits in western NL in July 2009. Sampling involved beach walks and/or snorkel surveys in the region of St. George's Bay, Port au Port Bay, Bonne Bay, and St. Paul's Inlet, in western NL. No recent fieldwork was conducted on the south coast of NL. In addition, to investigate distributional limits in the southwestern Gulf of St. Lawrence, in July 2010 we investigated the northern shore of the Baie des Chaleurs between Carleton and Pasbébiac, east of New Carlisle. Select beaches were surveyed for shells of *C. fornicata* through hour-long beach walks encompassing both the lower and higher regions of the shoreline.

RESULTS

Pre-1934 literature survey

The northern distribution of the slipper limpet has long been known to correspond with the so-called Virginian or warm-temperate fauna, which mainly ranges south of Cape Cod (Ganong 1887, 1890), but reappears north in the southwestern Gulf of St. Lawrence, the "Magdalen Shallows" enclave. The American oyster *Crassostrea virginica* (Gmelin, 1791) is the best known representative of this fauna, and *Crepidula fornicata* commonly attaches to oyster shells and other hard substrates (Galtsoff 1964).

The pre-1934 distributional records for *Crepidula fornicata* in eastern Canada are listed in chronological order in Table 1, beginning with Lyell (1841) who first noted the presence of *C. fornicata* in the Gulf of St. Lawrence. The

Table 1. Chronology of historical references (1841-1934) on the distribution of *Crepidula fornicata* in the Gulf of St. Lawrence, updated from Brunel *et al.* (1998).

Authors	Year	Original or translated quotations on localities and (notes)
Lyell	1841	"Gulf of St. Lawrence" (p. 138; without localities)
Bell	1859a	"One specimen found at Dalhousie, NB, very abundant at Caraquette" (p. 212; first locality on southwestern shore, second one on southeastern shore of Baie des Chaleurs)
Bell	1859b	"Dalhousie, Bay of Chaleur" (p. 254)
Gould and Binney	1870	"...on oysters from PEI, off the mouth of the St. Lawrence" (p. 271)
Dawson and Harrington	1871	"no dredging" (p. 50; only inshore sampling in Northumberland Strait)
Verrill *et al.*	1873	"...southern part of the Gulf of Saint Lawrence, PEI, &c" (pp. 649-650)
Whiteaves	1874a	"Between Cape Bear and Pictou Island" (p. 217) and "on oyster beds of Shediac Bay, N.B." (p. 217) (both in southeastern Northumberland Strait)
Whiteaves	1874b	"from the area between Prince Edward Island and Cape Breton, through Northumberland Straits, along the coast of New Brunswick as far to the north as the southern entrance to the Bay des Chaleurs; Carraquette Bay, N.B. seems to be their extreme northern limit." (p. 189) and cited in "...list of species collected in Shediac Bay" (p. 199)
Verrill	1879	(Listed for the area between Cape Cod and Gulf of St. Lawrence)
Bain	1885	(Recorded from PEI, without localities)
Whiteaves	1886	"Pictou, NS" (p. 28; southeastern Northumberland Strait)
Ganong	1887	"Dalhousie, Caraquette, (very abundant), Bell (C). Bay Chaleur, Whiteaves (D), Shediac, Whiteaves (I). Northumberland Straits and along the coast to Caraquette Bay, Whiteaves (H). Not found on the southern coast" (p. 38; letters between parentheses refer to bibliographic sources listed.)
Winkley	1888	"mostly from Summerside, PEI" (p. 69); "occurs in thousands" (p. 70)
Ganong	1890	(Species listed in table on p.172, under column "Gulf of St. Lawrence")
Provancher	1890	(Listed from the Province of Quebec, without localities)
Provancher	1891	"in southern part of Gulf of St. Lawrence, PEI, attached to various shells and especially oysters" (p. 88)
Winkley	1892	Among "colony of warm water shells in the waters of Northumberland Strait" (p. 63)
Conklin	1897	"...from Labrador to Florida" (p. 5; without localities)
Whiteaves	1901	"Abundant on oysters throughout the whole oyster region north-ward to Caraquette Bay" and "...in Northumberland Strait" (p. 168)
Chadwick	1906	"Bedeque Bay, common" (p. 103; PEI)
Halkett	1907	"Pictou, NS" (p. 347)
Ives	1907	"...quite common throughout the whole oyster region", "...not plentiful outside of low water mark" (typewritten copy seen only, with changed pagination; no specific reference to Northumberland Strait)
Stafford	1912a	"Malpeque" (p. 41, in checklist of species)
Stafford	1912b	"Canso, Malpeque" (p. 77; summary of earlier report)
Jones	1924	(from two stations) "Shippigan Gully... and Sound" (p. 2 + 16, northeastern NB, Baie des Chaleurs)
Dall	1926	"mouth of Burnt Church River, north side of Miramichi Bay, NB" (p. 153; none found in collections made in western NL)
Dall	1929	"Escuminac Point", NB (p. 159); "Buctouche", "beach at Cocagne Harbor", "beach at Grant (between Shemagoe Inlet and Cape Tormentine)", NB (p. 160)
Johnson	1934	"PEI to Texas and West Indies" (p. 97)

earliest detailed record of this species in the Gulf was provided by Bell (1859a), whose two localities placed the northernmost limit of *C. fornicata* along the southern shore of Baie des Chaleurs in NB, a region warmer than the northeastern shore of this bay in QC (Jones 1924, Tremblay 1944, Brunel 1959, Legendre and Watt 1970). Most subsequent records, including Ganong (1887), a reliable source for other marine molluscs along the NB coast, confirmed this species as abundant and

typical of the Magdalen Shallows, mostly around PEI and the Magdalen Islands. One exception to this pattern was Conklin (1897), who listed the geographic range of *Crepidula* to include "Labrador". Labrador at that time referred to a large part of the Quebec-Labrador peninsula, including the eastern reaches of the north shore of the Gulf of St. Lawrence—a region known locally as the "Lower North Shore" (J. Maunder, pers. comm.). The basis for Conklin's inclusion of Labrador in the range of *C. fornicata* remains uncertain since this record was not supported by additional information nor by the earlier and thorough survey of Packard (1863, 1867).

Post-1934 publications

Little was published in the primary literature on the distribution of *Crepidula fornicata* in eastern Canada between 1934 and 1950. This changed significantly in the 1950s with the hiring of zoologist Edward L. Bousfield at the National Museum of Canada (NMC). Bousfield's explorations of the intertidal fauna of the Canadian Maritime Provinces (Bousfield 1952, 1955a, Bousfield and Laubitz 1972) quickly added to the research collections of the NMC (now the Canadian Museum of Nature) with publications on the distributional ranges of a broad set of taxonomic groups, including molluscs. Since 1950, of the 46 publications listing the distribution of *C. fornicata* in eastern Canada (Table 2), only 22 were based upon actual sampling: the remaining ones contained secondary information of variable quality on the distribution of this species or simply repeated previous records by the same author. A majority of the new sources—16 out of 22—merely confirmed historical records that the distribution in the Gulf of St. Lawrence encompassed the area around PEI northward to the Miramichi Estuary as well as the Magdalen Islands (Table 1). Included in this, Bousfield (1952, 1955a, 1960) provided general information on the distribution which he assumed to fit into that of the Virginian "warm-water fauna" already known since Ganong (1887, 1890), but he listed no localities to support his claim.

Significant primary records during this period relevant to the distributional limits of *Crepidula fornicata* reported the species from Baie des Chaleurs (Corbeil 1953, Logie 1953, Ledoyer 1975, Schafer and Wagner 1978) as well as from new localities in western NL (Mercer 1970, Hooper 1975, Carter and McGregor 1979), and the Quebec Lower North Shore (D'Amours and Pilote 1982). Among secondary publications, only La Rocque (1953), Bousfield (1960), Brunel (1970a), Dunbar *et al.* (1980), and Brunel *et al.* (1998) correctly cited the known historical northern limit of *C. fornicata*'s distribution in Baie des Chaleurs (~48°N). In 1955, Bousfield (1955a) suggested that *C. fornicata* might be found as far to the northeast as Gaspé Bay (north of Baie des Chaleurs) where other Virginian species can be found, but in his 1960 publication limited their northern distribution to "Chaleur Bay". This modification was later supported by the absence of this species in Gaspé Bay despite extensive sampling by Brunel (1970b and unpub. data) and Ledoyer (1975). Recent publications focusing on northern Atlantic *Crepidula* have provided vague and somewhat misleading northern geographic range limits for *C. fornicata*, with the northernmost latitudinal boundaries associated with PEI (Hoagland 1977, Collin 2001) or NB (Escuminac Point, NB; Blanchard 1997). Collin (2003) categorized *C. fornicata*'s northern range as extending >50°N, presumably because of the higher latitudes associated with its introduced range in Europe (59°N, Blanchard 1997) rather than its long-known native geographic range reaching Baie des Chaleurs (Bell 1859a, 1859b, Whiteaves 1901) in the northwestern Atlantic. Only one record, cited in Bourget (1997), is known to be erroneous (Bourget, pers. comm.): recent *C. fornicata* specimens have never been taken in the St. Lawrence Estuary, despite intensive inshore and offshore collecting since 1929 (Brunel *et al.* 1998).

The earliest publication to suggest the presence of *Crepidula fornicata* along NL's coastline was Bousfield's (1960) field guide which included "southwestern Newfoundland" within the range of this species (Table 2). Because Bousfield's 1960 range extension did not cite additional information or reference museum specimens, this northern locality went unnoticed or unaccepted by many subsequent workers (*e.g.*, Hoagland 1977, Collin 2001). In 1968, Mercer (1970) also recorded *C. fornicata,* along with several other epibionts, growing on oysters introduced to Two Guts Pond (Port au Port Bay) as seed and adults from PEI in 1965. In 1975, Bousfield and Thomas described *C. fornicata* as a component of the "very eurytopic warm water species" of the Canadian Atlantic "in all warm-water areas, including the west coast of Newfoundland..." (p. 57), but failing to reach the St. Lawrence Estuary. *Crepidula fornicata* was first reported to the north in Lomond, Bonne Bay (49°27'N, 57°45'W) and St. Paul's Inlet (49°51'N, 57°47'W) by Hooper (1975) as part of an ecological and biological assessment of Bonne Bay (and surrounding regions) for the Canadian National Parks Service in the early 1970s. Carter and MacGregor (1979), in their survey of St. Paul's Inlet, documented the location of *C. fornicata* within the eastern arm of that inlet, based upon surveys in 1977-78. These latter reports and other grey literature focusing on the benthic marine molluscs of Newfoundland and Labrador were brought to wider attention by Gilkinson (1986).

Brunel *et al.* (1998) reported *Crepidula fornicata* along the northeastern QC coastline of the Gulf of St. Lawrence, within the region defined above as the Lower North Shore. This record was based upon an inshore scallop survey in August 1981 in which 200 dredge samples were taken across

Table 2. Chronology of recent references (1950-2009) on the distribution of *Crepidula fornicata* in the Gulf of St. Lawrence, updated from Brunel *et al.* (1998).

Authors	Year	Original or translated quotations on localities and (notes)
Miner	1950	"...from PEI to Texas..." (p. 629)
Bousfield	1952	"The beaches of the gulf coast of NS, NB, and PEI present an entirely different picture."... "Species very commonly encountered are...the slipper limpets (*Crepidula* spp.)..." (p. 191)
Corbeil	1953	(recorded from scallop survey westward from Carleton, QC, northwestern shore of Baie des Chaleurs, and Black Point, NB)
La Rocque	1953	"Chaleur Bay to Texas and West Indies" (p. 160)
Logie	1953	"at Shippigan this year the slipper limpet constituted an additional fouling organism for the first time in the writer's experience. " (p. 16)
Warburton	1953	"Malpeque Bay, PEI....Limpets of two species, *Crepidula fornicata* and *C. plana* often occur on such shells" (p. 21; *i.e.*, "*Cliona*-inhabited oyster shells")
Abbott	1954	"Canada to Florida and to Texas" (p. 170)
Bousfield	1955a	"The fourth subregion takes in the entire north shore of Chaleur Bay eastward to and including Gaspe Bay" and "Many southern marine species reach their northern limit of distribution here, viz the gastropods *Crepidula fornicata*..." (p. 100)
Walne	1956	"...from Escuminac Point, New Brunswick, (47°N.), and Summerside, Prince Edward Island, in Canada, to the Caribbean islands..." (p. 1)
Bousfield	1960	"Chaleur Bay to southwestern NL and NS" (p. 13)
Carbonneau	1967	"caught relatively frequently" (p. 22; in scallop survey off the Magdalen Islands, QC)
Brunel	1970a	(Listed on p. 21 from subtidal depths in Baie des Chaleurs and the Magdalen Islands, QC)
Mercer	1970	On oysters, "Two-Guts Pond", Port au Port (p. 25; southwestern NL)
Thomas	1970	"Smelt Creek (p. 2), Bideford Estuary" (p. 6 + 17; northwestern PEI)
Hughes and Thomas	1971a	(Appendices IIa-c: recorded on Paugh's Creek transect (6/15 stations), Fred England Bed transect (8/17 stations), Martin Bed transect (9/21 stations) and Totten Bed transect (42/51 stations), Bideford River Estuary, PEI)
Hughes and Thomas	1971b	Bedeque Bay (PEI)
Gosner	1973	"BV" (*i.e.*, "boreal, from Cape Cod to Labrador" + "Virginian, from Cape Cod to Cape Hatteras" (p. 263, somewhat updated from Johnson, 1934)
Abbott	1974	"Canada to Florida and to Texas"(p. 141)
Hooper	1975	"Lomond, Bonne Bay" and "St. Paul's Inlet" (p. 140; western NL)
Ledoyer	1975	(dredge haul off Miscou and Shippigan Islands, northeastern NB)
Wagner	1975	Strait of Canso (NS, southeastern tip of Gulf of St. Lawrence; full range of species given as 12°N to 48°N in table 6, p. 13)
Wagner	1976	Miramichi Estuary (northeastern NB)
Caddy *et al.*	1977	Northumberland Strait and Georgetown Bay, PEI (in table 4, p. 15)
Hoagland	1977	"...north to PEI" (p. 375; based on collections examined at major museums in the U.S., England and Germany)
Schafer and Wagner	1978	Eastern Baie des Chaleurs
Carter and McGregor	1979	St. Paul's Inlet (western NL) (map on p. 136)
Gosner	1979	"Gulf of Mexico north to Massachusetts Bay, locally to Gulf of St. Lawrence, in lower intertidal zone. Accidental in Europe." "...especially along protected bays and sounds." (p. 129)
Dunbar *et al.*	1980	(Dots on map: south of Magdalen Islands, Northumberland Strait and Caraquet area, southeastern shore of Baie des Chaleurs, Bonne Bay, western NL, based on published previous surveys)
Colodey *et al.*	1981	Off Buctouche and St-Édouard-de-Kent (northeastern NB, northern Northumberland Strait; on crabs caught in lobster traps)
Citarella	1982	Shediac Bay, NB (Veliger larvae in plankton)
D'Amours and Pilote	1982	Off La Tabatière, QC (scallop survey close to and off Lower North Shore of Gulf of St.Lawrence)
Bourget and Messier	1983	Grande Entrée harbour (Magdalen Islands, QC)
Élouard *et al.*	1983	Grande Entrée lagoon (Magdalen Islands, QC)
Lobban and Hanic	1984	North Rustico (north shore of PEI)
Wagner	1984	"Miramichi Inner Bay" (p. 4; NB)
Gilkinson	1986	(Primary records of Carter and McGregor 1979 and Hooper 1975 from NL)

Table 2. (Continued)

Authors	Year	Original or translated quotations on localities and (notes)
Citarella	1987	(Same data as in 1982 paper)
Munro and Gagnon	1989	Havre-aux-Basques lagoon and Grande Entrée harbour (Magdalen Islands, QC)
Anonymous	1997	(Site of Confederation Bridge, between Cape Tormentine, NB and Borden Point (Queens), PEI, Northumberland Strait)
Blanchard	1997	"...Escuminac Point (47°N) on the Canadian coastline.." (p. 110, based on Walne, 1956) and 59°N in Europe (fig. 2)
Bourget	1997	"Lower Estuary (north and south), Gaspé peninsula, NB, PEI" (p. 87)
Brunel *et al.*	1998	(Recorded from 5 biogeographic regions in Gulf of St. Lawrence: Baie-des-Chaleurs, Magdalen Islands, QC, around PEI, Lower North Shore of Gulf, QC and western NL)
Mitchell	1999	(Primary records of Hughes and Thomas, 1971a, 1971b, and Anonymous, 1997 and secondary ones of Dunbar *et al.* 1980 reviewed)
Collin	2001	"...from PEI, Canada, to the Bahamas" (p. 2259; based on Hoagland 1977)
Collin	2003	(Latitudinal range given in Appendix 1: between 20-30°N and >50°N)
Rosenberg	2009	Range: 48°N to 25°N; 97.2°W to 25°W; Distribution: Canada: NS, PEI, NB...

depths ranging from 7 to 82 m between Baie-des-Moutons (50°45'N, 59°01'W) and Saint-Augustin (51°13'N, 58°38'W) (D'Amours and Pilote 1982), but the exact sampling locations of *C. fornicata* were not recorded nor specimens retained. Twelve of these hauls were located in Baie des Ha! Ha! (51°00'N, 58°56'W) and nine were taken in Kecarpoui Bay (51°04'N, 58°50'W), both of which are sheltered inlets and the most likely collection sites for this species.

Data in museum and field samples

Our survey of 12 collections confirmed the general geographic pattern of *Crepidula fornicata* from our literature review (Fig. 1), with the exception of the Lower North Shore of QC for which no corresponding museum specimens could be located. In addition, museum records from along the western and eastern shores of the Gulf of St. Lawrence and southern NL coast revealed that the distribution of *C. fornicata* extends further north, northwest, and east in Canadian waters (Tables 3-4) than recognized in the recent malacological literature. With reference to the western Gulf of St. Lawrence, museum collections in the CMN still retain two of the oldest samples of *C. fornicata* collected by Bell (1859a) on the southwestern and southeastern NB shores of Baie des Chaleurs (Table 3). One of these two localities, Dalhousie NB, lies approx. 120 km inside Baie des Chaleurs from Caraquet, NB, and the associated CMN specimen (ML073451) represents the extreme northwestward limit to the distribution of *C. fornicata* in the Gulf of St. Lawrence. It is remarkable that all subsequent authors until now (Tables 1-2) have ignored the significance of this locality. Nine samples recorded in Table 3, including four collected in 2010, also extend the distribution of the species onto the northern QC shore of Baie des Chaleurs, as far as New Carlisle, in the middle of the QC shore of the bay. Only one of these nine lots is associated with a research publication (Corbeil 1953); the particular station where *C. fornicata* was dredged, however, is not specified either in the paper or on the museum label, but Corbeil's comments suggest that it may have been off Carleton, on the QC shore. In 2010, one beach walk was conducted along the shell-rich beach of Pasbébiac, east of New Carlisle; however, no *Crepidula fornicata* were found. Consequently, New Carlisle remains the furthest east along the northern QC shore of this bay where this species has been reported.

Consideration was given to mapping all null records of *Crepidula fornicata* in the western part of the Gulf of St. Lawrence, in the St. Lawrence Estuary, the Saguenay Fjord, and the North Shore of the Gulf to provide additional evidence of the distinct biogeographic boundary in this region. This would have been a formidable task, however, given the thousands of samples of benthic fauna that have been collected over the past century, spanning from the intertidal zone to the greatest depths of the Laurentian Channel (Brunel *et al.* 1998). Our reliance on positive records is thus dependent on the assumption that these coastlines and shallow water marine environments have been sufficiently explored such that if this species was present, it would have been detected.

Museum records for the eastern-most range of *Crepidula fornicata*'s distribution in NL (Table 4) also deserve special attention. Of 130 collection lots of *C. fornicata* in the CMN—by far the most significant collection of eastern Canadian *Crepidula*—two are lots collected from the southwestern coast of NL in Port au Port Bay. Likewise, the NFM currently houses 17 lots of *C. fornicata*, of which 12 are from the southern and southwestern shores of NL. The earliest record of *Crepidula fornicata* in NL is labelled "*Crepidula*" collected

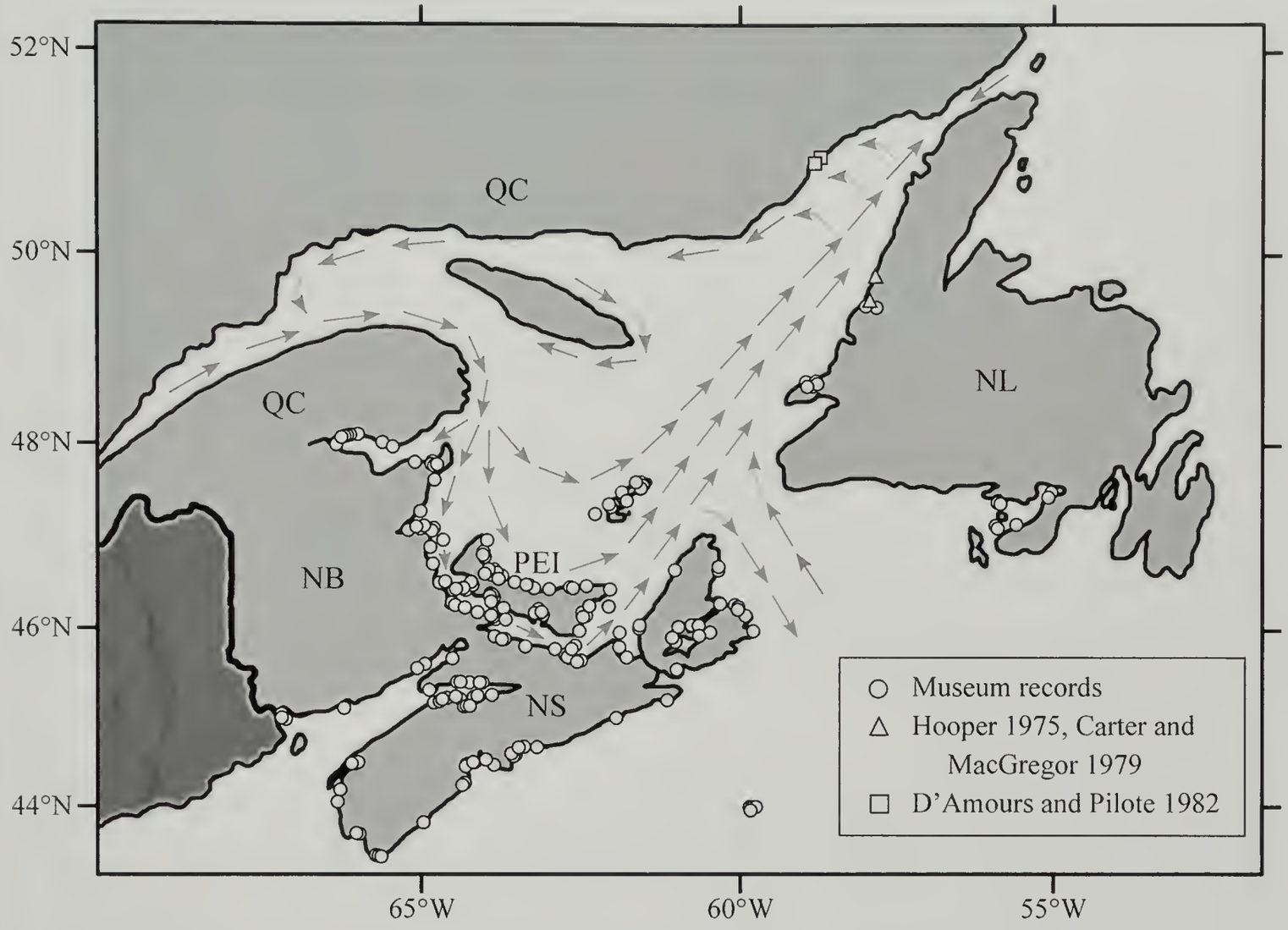

Figure 1. The distribution of *Crepidula fornicata* in eastern Canada based on collection records (1858-2010) from 12 museums in Canada and the U.S., three literature sources, and personal collections made in 2009 and 2010 (now deposited in the CMN and IQBIO). Canadian museums surveyed included the ARC, CMN, MLI, NFM, NSMNH, and ROM; U.S. museums included the AMNH, ANSP, FMNH, MCZ, NMNH, and PMNH. Where specific coordinates were associated with collection localities they were used to plot symbols. However, for many museum lots only general locality information was available for mapping. Three literature sources were also used to provide locality information for specimens of *C. fornicata* not vouchered in museum collections: Hooper 1975 (Bonne Bay and St. Paul's Inlet, NL), Carter and MacGregor 1979 (St. Paul's Inlet, NL), and D'Amours and Pilote 1982 (Lower Quebec North Shore, QC). Although specific stations associated with *Crepidula* were not noted by D'Amours and Pilote (1982), the mapped symbols represent the most likely collection localities within their broad geographic sampling of this region. Arrows represent the typical summer surface water circulation patterns within the Gulf of St. Lawrence (Koutitonsky and Bugden 1991).

at "Two Guts Pond" (48°39'N, 58°40'W), Port au Port Bay, southwest NL, by E. L. Bousfield on July 17, 1954 (CMN ML055736; Table 4). This specimen probably contributed to the change in his range description for *C. fornicata* from 1955a to 1960 to include "Chaleur Bay, NB, to southwestern Newfoundland and Nova Scotia" (Bousfield 1960). Specimens of *C. fornicata* were collected again in Port au Port Bay on June 6, 1966 by D. E. McAllister and W. Van Vliet (CMN ML091501). Beach-collected *C. fornicata* shells from Port au Port Bay are represented in the NFM collections from 1971 onwards (Table 4) and we have collected shells from this region as recently as July 2009 (shell lengths from 37.0 to 42.0 mm, $N = 3$). This 2009 sample has now been deposited at the CMN (Table 4). Although we were unable to locate any museum specimens from farther north on the western shores of NL, including Bonne Bay or St. Paul's Inlet, we collected live *C. fornicata* in Lomond, Bonne Bay, in July 2009, and specimens have also been observed and collected in other regions of Bonne Bay in 2009 (Table 4; Robert Hooper, pers. comm.). Live specimens from Bonne Bay ranged in shell length from 21.6 to 43.2 mm ($N = 4$) suggesting that these had survived at least one winter; in addition, two individuals

Table 3. Chronological data documenting selected museum samples of *Crepidula fornicata* near the northern limit of its distribution along the western shores of the Gulf of St. Lawrence, north of Pointe Sapin, NB (46°58'N, 64°50'W).

Museum[1]	Cat. No.	Date	Locality	Geographic coordinates[2]	Collector[3]	Reference
CMN	ML073451	1858[4]	Dalhousie, NB ("Bay of Chaleur", southwestern shore)	[48°04'N, 66°23'W]	RB	Bell 1859a, 1859b
CMN	ML073457	1858[4]	Caraquet, NB ("Carraquette Bay, Bay of Chaleur", southeastern shore)	[47°48'N, 64°57'W]	RB	Bell 1859a
CMN	ML091184	1950-07-28	Off Munro Island, Shippigan Bay, NB	47°45'N, 64°47'W	ELB	
CMN	ML091160	1950-08-29	Off Point aux Carr, Miramichi Bay, NB	47°05'N, 65°13'W	ELB (Stn M-140)	Bousfield 1955b (map of stations)
CMN	ML055659	1950-08-30	Off Egg Island, Miramichi Bay, NB	47°06'N, 65°03'W	ELB (Stn M-147)	Bousfield 1955b
CMN	ML091198	1950-08-30	Off Île du Vin, Miramichi Bay, NB	47°06'N, 65°05'W	ELB (Stn M-121a)	Bousfield 1955b
CMN	ML055661	1950-08-30	Off Hardwicke, Miramichi Bay, NB	47°05'N, 65°01'W	ELB (Stn M-151)	Bousfield 1955b
CMN	ML091164	1950-08-31	Off Escuminac Village, NB (southeast Miramichi Bay)	47°05'N, 64°55'W	ELB (Stn M-162)	Bousfield 1955b
NMNH	366211	1950-08	Escuminac Point, NB (southeast Miramichi Bay)	[47°04'N, 64°47'W]	ELB (Stn. M-108)	Bousfield 1955b
MLI	(Acc. 2208)	1952-10	Between Carleton, QC and Miguasha Point, QC, western Baie des Chaleurs[5]	48°05'N, 66°10'W	HEC (MAPAQ Stn D42)	Corbeil 1953 (basis for Brunel 1970a)
CMN	ML031227	1960-08-04	North channel of lagoon, Tracadie Bay, NB	47°33'N, 64°53'W	ELB (Stn B-13)	
CMN	ML038997	1960-08-05	St. Simon Inlet, Shippigan Bay, NB	47°45'00"N, 64°49'00"W	ELB (Stn B-17)	
CMN	ML073442	1961-07-13	"MRC de Bonaventure" (northwestern Quebec shore of Baie des Chaleurs)	[48°05'N, ~66°W]	AET	
CMN	ML067226	1966-07-20	St. Simon Inlet, Shippigan Bay, NB	47°46'00"N, 64°46'00"W	MLHT	
CMN	ML067153	1966-07-21	West side of Brule Point, Pointe-Brûlé, Shippigan Bay, NB	[47°45'36"N, 64°44'49"W]	MLHT	
CMN	ML067270	1966-07-21	Neguac Plots, NB (north of Miramichi Bay)	47°15'N, 65°05'W	MLHT	
MLI	(Acc. 410)	1982-09-01	New Carlisle, QC (north shore of Baie des Chaleurs)	48°00'15"N, 65°23'00"W	DDA	
CMN	ML092899	1990-08-11	Beach at Carleton, QC (northwestern shore of Baie des Chaleurs)	[48°06'N, 66°08'W]	MC	
FMNH	282288	2000	Escuminac Point, NB (southeast Miramichi Bay)	47°06'N, 64°49'W	DV (DV-282288)	Collin 2001
IQBIO[6]	41-	2000-08-01	Subtidal sand with *Zostera* at Carleton, QC	48°06'44"N, 66°08'48"W	PB	
IQBIO	41-	2010-07-27	Subtidal sand with *Zostera* at Carleton, QC	48°05'44"N, 66°08'48"W	PB	
IQBIO	41-	2010-07-28	Beach east of Carleton, QC	48°06'00"N, 66°04'40"W	PB	
IQBIO	41-	2010-07-29	Beach west of New Richmond, QC	48°10'22"N, 65°53'02"W	PB	
IQBIO	41-	2010-07-29	Beach south of Bonaventure, QC	48°01'28"N, 65°28'23"W	PB	

[1]Museum abbreviations: CMN, Canadian Museum of Nature; FMNH, Field Museum of Natural History; IQBIO, Institute Québécois de la Biodiversité; MLI, Maurice Lamontagne Institute; NMNH, National Museum of Natural History. [2]Geographical coordinates enclosed in brackets were approximated based on site locality information. [3]Author abbreviations: RB, R. Bell; ELB, E. L. Bousfield; HEC, H.-É. Corbeil; AET, A. E. Tener; MLHT, M. L. H. Thomas; DDA, D. D'Amours; MC, M. Castonguay; PB, P. Brunel; DV, D. Véliz. [4]Listed as 1866 in museum records; however, Bell, who sampled molluscs in this bay in 1858, is not known to us to have been there in 1866. The number of specimens agrees with Bell (1859a); [5]Locality based on notes in Corbeil (1953) pertaining to 14 species of molluscs collected: "a small number of specimens were taken", and "apart from a few specimens dredged in the deeper muddy areas, molluscs are encountered mostly near shore, and in five sections off Carleton." (p. 63); [6]Provisional storage of a private collection in MLI started in October, 2008; final catalogue numbers have yet to be assigned.

Table 4. Chronological data documenting selected museum samples of *Crepidula fornicata* near the northeastern limit of its native distribution in western and southern Newfoundland (NL).

Museum[1]	Cat. No.	Date	State	Locality	Geographic coordinates[2]	Collector[3]	Reference
CMN	ML055736	1954-07-17	Wet	Two Guts Pond, Port au Port Bay, W NL	48°39'N, 58°40'W	ELB (StnW-12)	Bousfield 1960
CMN	ML091501	1966-06-09	Dry	Port au Port Bay, (park at S end of W. Bay), W NL	[48°33'31"N, 58°54'26"W]	DEM, WVV	
NFM	MO-1974	1971	Dry	1.5 miles NE of Harbour Mille, NE Fortune Bay, S NL	[47°35'18"N, 54°51'20"W]	JEM, RGN	
NFM	MO-1980	1971	Dry	Grand Beach, Fortune Bay, S NL	[47°08'33"N, 55°31'20"W]	RGN	
NFM	MO-1981	1971	Dry	Piccadilly, Port au Port Bay, W NL	[48°33'28"N, 58°54'16"W]	RGN	
NFM	MO-1975	1980	Dry	Southern Fortune Bay, S NL	[47°10'N, 55°46'W]	TA	
NFM	MO-1976	1980	Dry	Southern Fortune Bay, S NL	[47°10'N, 55°46'W]	DM	
NFM	MO-1982	1982	Dry	Harbour Breton, Fortune Bay, S NL	[47°28'56"N, 55°47'48"W]	RGN	
NFM	MO-1977	1983	Dry	Boswarlos, Port au Port Bay, W NL	[48°34'10"N, 58°48'55"W]	RGN	
NFM	MO-501	1984	Dry	Black Point, Port au Port Bay, W NL	[48°36'16"N, 58°41'10"W]	JEM	
NFM	MO-502	1984	Dry	West Bay Beach, Port au Port Bay, W NL	[48°35'54"N, 58°56'16"W]	JEM, BW	
NFM	MO-1768	1988	Dry[4]	Piccadilly, Port au Port Bay, W NL	[48°33'28"N, 58°54'16"W]	JEM	
NFM	MO-1978	1995	Dry	Little Bay East, NE Fortune Bay, S NL	[47°33'29"N, 54°50'54"W]	JEM	
NFM	MO-1979	1998	Dry	Harbour Breton, Fortune Bay, S NL	[47°28'56"N, 55°47'48"W]	RGN	
CMN	ML094274	2009-05	Wet	Norris Point, Bonne Bay, Gros Morne National Park, W NL	49°31'03" N, 57°52'33"W	RH	Present paper
CMN	ML094275	2009-07-20	Dry	Port au Port Bay, (park at S end of E. Bay), W NL	48°33'32" N, 58°43'47"W	TAR, JMA, and MJM	Present paper
CMN	ML094276	2009-07-21	Wet	Lomond, Gros Morne National Park, W NL	49°27'44" N, 57°45'38"W	TAR, JMA, and MJM	Present paper

[1]Museum abbreviations: CMN, Canadian Museum of Nature; NFM, The Rooms Provincial Museum. [2]Geographical coordinates enclosed in brackets were approximated based on site locality information. [3]Collector abbreviations: BW, B. Withycombe; DM, D. Manuel; DEM, D. E. McAllister; ELB, E. L. Bousfield; JMA, J. M. Aker; JEM, J. E. Maunder; MJM, M. J. MacInnis; RGN, R. G. Noseworthy; RH, R. Hooper; TA, T. Ansty; TAR, T. A. Rawlings; WVV, W. Van Vliet; [4]Subfossil: based on a visual evaluation by J. Maunder, NFM.

forming a stack were both found to be brooding eggs. Two voucher shell lots from this region, including material preserved in alcohol, are now deposited at the CMN (Table 4).

The NFM also retains 7 lots of *C. fornicata* from along the southern shores of NL. These localities are not currently reflected in any primary research publication. The earliest records date to 1971 when two collections of *C. fornicata* were made in southeastern and northeastern Fortune Bay, on the southern coast of NL (Fig. 1; Table 4). Subsequent collections have been made in other areas of Fortune Bay, the most recent in 1998 (Table 4). In October 2007, *C. fornicata* was also observed on mussel shells in Pool's Cove, Fortune Bay, by a field researcher at Memorial University's Ocean Sciences Centre (Philip Sargent, pers. comm.).

DISCUSSION

Museum collections have long been employed to document changes in the geographic distribution and morphology of marine gastropods through time (*e.g.*, Vermeij 1982, Seeley 1986, Carlton *et al.* 1991, Fisher *et al.* 2009). Here, we have used records from 12 museums, supplemented with a literature review and new collections, to clarify the present distribution of a well-known shallow water marine gastropod, *Crepidula fornicata*, in the northwestern Atlantic. Our results extend the northern distribution of *C. fornicata* in eastern Canada potentially as far north as 51°N latitude and as far east as 55°W. Although the northern distribution of *C. fornicata* is still substantially lower than the 59°09'N achieved by introduced *C. fornicata* in Oslo Fjord, Norway (Blanchard 1997), northeastern Atlantic water temperatures are typically warmer at a given latitude than in the northwestern Atlantic. As for many other intertidal and shallow marine organisms, water temperature likely plays an important role in limiting the northerly distribution of *Crepidula* (Hutchins 1947, Bousfield and Thomas 1975, Southward *et al.* 1995, Therriault and Herborg 2008). Thieltges *et al.* (2004) have associated cold temperatures with heavy winter mortality and low abundance of *C. fornicata* in the northern Wadden Sea of Germany (54°49'–55°09'N), where long-term average water temperatures range from 2.7 °C in February to 18.1 °C in August. Abundance of *Crepidula* barely reaches 100/m^2 at this latitude compared to >1000/m^2 in more southern localities in Europe, and overwinter mortalities can reach 97% in some mussel beds (Thieltges *et al.* 2004). Mortality is assumed to be the result of ice scour or direct exposure to low temperatures, particularly during aerial emersion in intertidal or shallow subtidal habitats.

The distribution of *Crepidula fornicata* in the northwestern Atlantic likely reflects: (1) long-term post-glacial changes in the Canadian Atlantic, (2) seasonal physical conditions within shallow water marine habitats, (3) physiological tolerances to water temperature, salinity, and dissolved oxygen, and (4) current patterns associated with larval delivery. Environmental niche modeling (Therriault and Herborg 2008) can help to link known localities of a species to critical environmental parameters in order to predict its potential distribution. The output of such models often predicts the non-contiguous distribution of a species (Therriault and Herborg 2008), where its presence is associated with patches of favourable physical conditions (Bousfield and Laubitz 1972). Such modeling appears most effective when it incorporates seasonal variation in temperature and salinity rather than summer or winter values alone. In the shallow water suspension-feeding ascidian *Ciona intestinalis*, of 10 environmental variables used to predict the distribution, three variables (October – December water temperature, October – December salinity, and January-March water temperature) were the highest contributors to model accuracy (Therriault and Herborg 2008).

While niche modelling has yet to be done for *Crepidula fornicata*, the distribution of this species in eastern Canada does correspond with surface water temperatures. Within the southwestern Gulf of St. Lawrence, for instance, the northern distribution of *C. fornicata* ends at the middle of the north shore of Baie des Chaleurs near New Carlisle, QC (Fig. 1). The abrupt end to its distribution is associated with the presence of significantly colder waters in the northeastern, open portion of Baie des Chaleurs (Bousfield and Thomas 1975). A branch of the cold Gaspé Current moves westward along the northeastern QC shore of this bay (Tremblay 1944, Brunel 1959) and deviates into a cyclonic gyre in the middle of the bay (Legendre and Watt 1970). The abundance of collection records of *C. fornicata* in the warm southern Gulf, Bras d'Or lakes, and Minas Basin, corresponds with the presence of warm (>18 °C) summer surface waters (Bousfield and Thomas 1975). This pattern is not absolute, however. *Crepidula fornicata* occurs in near shore environments with colder summer water temperatures, including the Magdalen Islands, Cape Breton Highlands and Sydney Bight (15-18 °C), as well as the outer coast of NS, including the Bay of Fundy (12-15 °C) (Bousfield and Thomas 1975). In these localities, *C. fornicata* is apparently confined to sheltered inlets and bays where temperatures are warmer (Bousfield and Laubitz 1972). In NL, *Crepidula* is now known to be associated with the warmer summer waters of Port au Port Bay (15-18 °C) on the southwestern coast, and within bays and inlets of Fortune Bay on the southern coastline, where the summer temperature range is typically 12-15 °C (Bousfield and Thomas 1975). This summer temperature range also corresponds to localities of *Crepidula* in Bonne Bay and St. Paul's Inlet on the west coast. In Bonne Bay, surface water temperatures typically range from -1 to 16-18 °C (Hooper 1975), corresponding well with

our collection of *C. fornicata* in Lomond, July 21, 2009, where water temperature was 14.8 °C (0.5 m depth). Likewise, Carter and MacGregor (1979) reported typical summer surface water temperatures of ≤15 °C in St. Paul's Inlet during their 1977-78 sampling.

The discovery of *Crepidula fornicata* along the Lower North Shore of QC (D'Amours and Pilote 1982; "BCN" in Brunel *et al.* 1998) is the most surprising distributional record of *C. fornicata* based upon water temperature. This region is generally the coldest area of the Gulf of St. Lawrence, receiving icebergs from Labrador through the Strait of Belle Isle, with summer surface temperatures typically below 12 °C (Bousfield and Thomas 1975, Brunel *et al.* 1998). Nevertheless, the Lower North Shore also has numerous sheltered bays and inlets. Growth rates of giant scallop (*Placopecten magellanicus* (Gmelin, 1791)) in this region can also be very high, suggesting that warm plankton-rich microclimates, suitable for other suspension-feeding organisms such as *Crepidula*, are present locally (Pilote, pers. comm.).

Has *Crepidula fornicata* expanded its distribution into NL and the northeastern Gulf of St. Lawrence within the past 50 – 60 years, or are these new records simply a reflection of wider geographic sampling? The sub-fossil *C. fornicata* shells collected in 1988 from Picadilly, Port au Port Bay (J. Maunder, pers. comm., Table 4), suggest that this species has existed along the NL coastline in the past. These undated fossils are not necessarily reflective of the long-term presence of this species in Port au Port Bay, however, and may indicate their transient presence during past periods of warmer ocean temperatures (Bousfield and Thomas 1975). The first recent evidence of *C. fornicata* in NL, beyond Baie des Chaleurs, QC, was one lot collected by Bousfield from Port au Port Bay in 1954, followed by collections by McAllister and Van Vliet in 1966, and observations by Mercer in 1968. In part, the prior absence of records in NL may reflect the dearth of interest in non-commercial benthic marine molluscs of Newfoundland and Labrador in the 1900s (Gilkinson 1986; but see Dall 1926). The rugged coastline of NL, particularly the southern coast between Port aux Basques and Fortune Bay, has also limited surveys, and is the most poorly studied coastal region of NL (Gilkinson 1986). An additional factor may be the low population density of this species in NL. In areas that we have sampled, this species is simply not as abundant as in similar habitats at lower latitudes and does not appear to contribute to beach shell debris to the same extent as it does further south. Hence, this species is much less conspicuous within the northern extremes of its range in the northwestern Atlantic.

The planktotrophic development of this species and its long larval life of several weeks (Pechenik 1990) nevertheless provide opportunity for *Crepidula fornicata* to exploit new environments when conditions are suitable. The rapid spread in its introduced range in Europe is due in part to dispersal of larval stages (Blanchard 1997). The direction of surface currents, irrespective of temperature, may either stop or enhance larval dispersal. For instance, the branch of the cold Gaspé Current which deviates westward into the northeastern half of Baie des Chaleurs due to the Coriolis effect (Tremblay 1944, Brunel 1959) may well shift larvae into the central cyclonic gyre (Legendre and Watt 1970) and carry them back toward the southeastern or southwestern shores of the bay. In contrast, the August circulation off the western NL shore is clearly directed toward the Lower North Shore of the Gulf of St. Lawrence (El-Sabh 1976, Koutitonsky and Bugden 1991) in the most propitious season. This pattern of currents, coupled with the favourable inlet habitats along this coastline, could thus explain the surprising occurrence of *C. fornicata* in this otherwise cold environment.

Crepidula fornicata has also had a long history of human-mediated range expansion through the transport of oysters and mussels for aquaculture as well as via the fouling of boat hulls (Carlton 1992, Blanchard 1997, Collin *et al.* 2006). Aquaculture operations, such as introduction of oysters into habitats of the QC shore of Baie des Chaleurs (Corbeil 1948, 1949) and in Port au Port from PEI (Mercer 1970), could certainly have introduced *Crepidula* to the northern shores of Baie des Chaleurs and to NL. Unsuccessful introduction of oysters in the Port-Daniel lagoon, northeastward from New Carlisle, could nevertheless have allowed larvae to drift back westward, and may have helped establish the species in New Carlisle. The first observation of *Crepidula* in Two Guts Pond, NL, however, precedes any known oyster introduction to western NL. Other oyster introductions are also known to have occurred in other regions of NL (Mercer 1970) although details of these are lacking. Both natural and human-mediated transport could thus be responsible for the spread of this species in NL and QC.

Interestingly, *Crepidula plana*, the only other common species of *Crepidula* in the Gulf of St. Lawrence, does not appear to be present in NL or the northern Gulf. This species can be found sympatrically with *C. fornicata* in some habitats in NS (T. Rawlings and J. Aker, pers. obs.), but appears to have a more restricted geographic distribution within the Gulf (Brunel *et al.* 1998). Differences in the spread (and invasion potential) of these two species have also been noted elsewhere. At least one specimen of *C. plana* was introduced into Ireland in 1865 (Blanchard 1997), but this species never became established. In contrast, Europe continues to live with the consequences of the introduction of *C. fornicata* in the late 1800s.

In summary, clarification of a species' geographic range, as attempted here for *Crepidula fornicata*, remains an important task for establishing temporal benchmarks against which to assess the effect of climate change on the marine

environment. To continue this process in eastern Canada, further exploration of the long-neglected rugged coastlines of the northern shores of the Gulf of St. Lawrence, and around NL, is clearly needed, with emphasis on the collection and preservation of voucher specimens of near-shore species, and the careful documentation of collection localities and associated physical variables.

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